Muzzle size, paranasal swelling size and body mass in *Mandrillus leucophaeus*

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Abstract

The drill (*Mandrillus leucophaeus*), a forest-living Old World monkey, is highly sexually dimorphic, with males exhibiting extreme secondary sexual characteristics, including growth of paranasal swellings on the muzzle. In this study, the size of the secondary bone that forms the paranasal swellings on the muzzles of drills was assessed in relation to body mass proxies. The relationship between the overall size of the muzzle and surrogate measures of body mass was also examined. In female drills, muzzle breadth was positively correlated with two proxies of overall body mass, greatest skull length and upper M1 area. However, there was no such correlation in males. Paranasal swellings in males also appeared to have no significant relationship to body mass proxies. This suggests that secondary bone growth on the muzzles of male drills is independent of overall body size. Furthermore, this secondary bone appears to be vermiculate, probably developing rapidly and in an irregular manner, with no correlation in the sizes of paranasal swelling height and breadth. However, various paranasal swelling dimensions were related to the size of the muzzle. It is suggested that the growth of the paranasal swellings and possibly the muzzle could be influenced by androgen production and reflect testes size and sperm motility. The size and appearance of the paranasal swellings may thus be an indicator of reproductive quality both to potential mates and to male competitors. Further work is required to investigate the importance of the paranasal swellings as secondary sexual characteristics in *Mandrillus*, and the relationship between body size and secondary sexual characteristics. Attention should also be paid to the mechanisms and trajectories of facial growth in *Mandrillus*.

Key Words: Drill, mandrill, Cercopithecidae, muzzle, craniofacial morphology, body size

Introduction

The drill, *Mandrillus leucophaeus* (Primates, Cercopithecidae), is one of the largest extant monkey species and also one of the most sexually size dimorphic (HILL, 1970; SETCHELL *ET AL.*, 2000). Adult males also exhibit striking secondary sexual characteristics, including colouration of the perineal region and fat gain on the rump. A high level of sexual dimorphism and development of distinctive masculine secondary sexual characteristics is also evident in the other member of the genus, the mandrill (*M. sphinx*). An important characteristic of both the drill and the mandrill, largely absent in other big cercopithecids, is paranasal swelling of the muzzle. This feature is much larger in males than in females. In male mandrills it is accompanied by bright blue and red colouration of the facial skin, but this is not seen in male drills, where the paranasal region is jet black (HILL, 1970).

Secondary sexual characteristics and adornments are not unusual in males. Such traits have been recorded in insects, birds, fishes and mammals, acting as signals of reproductive quality to potential mates or being important in male-male competition (MALO *ET AL.* 2005). Despite their striking appearance, little is known about the mechanisms surrounding the growth and development of the *Mandrillus* muzzle and paranasal swellings. The role of the highly-elaborated muzzle in reproductive success is also not fully understood. What little research there has been focuses on the mandrill, and very few field studies of drill ecology, biology or behaviour have been carried out (GARTLAN 1970; WILD *ET AL.* in press). In *M. sphinx*, muzzle dimensions do not correlate with body size or social status (WICKINGS & DIXSON 1992 a & b). This finding poses interesting questions concerning selection for large muzzles in *Mandrillus* and about the underlying mechanisms that control growth and development in this region.

In this study, the relationships between the size of the paranasal swellings, the size of the muzzle and body size surrogates are examined in a sample of crania from free-ranging *M. leucophaeus*, collected in Cameroon. It is commonly assumed that the biology and behaviour of the drill is very similar to that of the mandrill, so the patterns observed in the drill sample are compared to findings from studies of living mandrills (WICKINGS & DIXSON 1992 a & b), to assess whether the relationships between muzzle size, paranasal swelling size and overall body size are similar in the two species.

Methods

The sample comprised 34 adult *M. leucophaeus* crania collected from village localities in Cameroon and held in the collections of CRES Cameroon. All were originally from wild-living populations and are likely to have been collected by villagers over a considerable period of time before being donated to the CRES collection. Maturity of each individual was assessed on the basis of M3 eruption. The sample was divided unequally by sex, with 7 female specimens and 27 male specimens. Due to damage, some specimens were excluded from certain analyses.

Data were collected using digital calipers on upper M1 length and breadth, greatest skull length, muzzle length and muzzle breadth at P3, M2 and M3. Upper M1 length was measured as the maximum mesiodistal length of the tooth and breadth was measured as the maximum buccolingual dimension. The product of these two measurements was used to represent upper M1 area. Greatest skull length was measured from the alveolar point to inion and muzzle length was taken from the alveolar point to nasion, both as described in FREEDMAN (1957). Muzzle breadth was taken between the lateral surfaces of the maxillae, again following FREEDMAN (1957), at the levels of P3, M2 and M3. In males, height and breadth of the paranasal swellings at M2 and M3 were also collected, taken as shown in Figures 1a and 1b.

FIGURES 1a AND 1b HERE

All statistical tests were performed in SPSS 11.5. The data were analyzed for departures from normality using Shapiro-Wilk *W* tests. In the pooled male and female sample, there was a clear bimodal distribution by sex, but when analyzed separately all the female data were normally distributed. In males, the only data that differed significantly ($p < 0.05$) from a normal distribution were the breadth of the paranasal swellings at M2 and M3, so these two measurements were analyzed using non-parametric statistics. Differences in craniodental dimensions, including muzzle size, between males and females were assessed using independent samples t-tests. In the absence of data on actual body masses or other whole-body size measures (such as crown-rump length), two body mass proxies (after ELTON *ET AL*., 2001) were used in analysis: upper M1 area, found by DELSON *ET AL.* (2000) to have a strong relationship with body mass in male and female cercopithecids, and greatest skull length. The relationships between muzzle length and breadth and the two body size proxies were examined in the pooled sample of males and females as well as in each sex separately, using the parametric Pearson product-moment correlation or the non-parametric Spearman's rho as appropriate. Analysis of the male skulls was extended to investigate the relationships between paranasal swelling sizes and muzzle length and breadth, and between paranasal swellings and the body mass proxies, again using the Pearson product-moment correlation or Spearman's rho as appropriate. As the purpose of the analysis was to investigate how the size, rather than the shape, of the paranasal swellings related to skull size and body mass proxies, only raw data were used, and no size correction methods were applied to any of the measurements.

Results

The sexual dimorphism that is characteristic of *Mandrillus leucophaeus* is clearly evident from the craniodental dimensions and t-test results reported in Table 1. Of particular relevance to this study, the male muzzle is significantly longer and broader than the female muzzle (Table 1, Figure 2). In the pooled male / female sample, there are significant correlations (Table 2, Figure 2) between muzzle length and breadth at M2, M3 and P3. These relationships are not significant when the sample is split by sex (Tables 2 and 3), although r values are higher in females than in males.

TABLES 1, 2 & 3 HERE

FIGURE 2 HERE

There was no significant correlation between muzzle length and the body mass proxy upper M1 area in the pooled male / female sample (Table 2) nor in the separate sexes (Tables 2 and 3). In females, muzzle breadths at M3 and P3 (but not M2) were significantly positively correlated with the two body mass proxies upper M1 area and greatest skull length (Table 2). However, in the male sample there was no significant correlation between muzzle breadths at M3, M2 or P3 and either of the two body mass proxies (Table 3).

Male paranasal swelling breadths at M2 and M3 were distributed bimodally (Figure 3 depicting the distribution for the paranasal swelling breadths at M2). No other craniodental dimensions, including the heights of the paranasal swellings, deviated from a normal distribution, as indicated by the Shapiro-Wilk *W* tests described in the Methods section. There was a significant positive correlation between paranasal swelling breadths at M2 and M3 (Table 3) and also between paranasal swelling heights at M2 and M3 (Table 3). No significant correlation was found between paranasal swelling breadth and height at either M2 or M3. Paranasal swelling height at both M2 and M3 correlated positively and significantly with muzzle length, and paranasal swelling breadth at M3 was significantly positively correlated with muzzle breadth at M2. However, there was no significant correlation between either paranasal swelling breadth or height and upper M1 area or between paranasal swelling breadth or height and greatest skull length in males (Table 3).

FIGURE 3 HERE

Discussion

The drill (*Mandrillus leucophaeus*) is a highly sexually dimorphic monkey (HILL, 1970; SETCHELL *ET AL*., 2001), and this dimorphism, as might be expected, is evident craniofacially. In the drill sample studied here, female greatest skull length is significantly smaller than male skull length, and female muzzles are, on average, only 70% the length and breadth of those in males. In papionins as a whole, the male muzzle is relatively more prognathic, larger and deeper than in females (O'HIGGINS & COLLARD, 2002), and this is certainly the case in *M. leucophaeus*.

It has been shown in longitudinal studies of sedated animals that during puberty muzzle lengths and breadths in male mandrills (*M. sphinx*) grow in proportion to body length (WICKINGS & DIXSON, 1992b). However, it has also been reported that muzzle lengths in adult male mandrills do not correlate with body mass, body length or social status (WICKINGS & DIXSON, 1992a). The data used in the present study are taken from skeletal material, and thus do not include measures of body mass or stature. It is possible, however, to use certain cranial dimensions that are highly correlated with actual body mass as body mass proxies (ELTON *ET AL*., 2001). Of the two body mass proxies used, the area of the upper first molar is likely to be the most appropriate when examining muzzle morphology as it is more independent of facial characteristics than is greatest skull length. The cross-sectional data for *M. leucophaeus* indicate that, at least in adulthood, male muzzle length is not significantly correlated with upper M1 area, and so is unlikely to be correlated with actual body mass. This result agrees with that observed in *M. sphinx* (WICKINGS & DIXSON, 1992a). Similarly, there is no correlation between muzzle breath and upper M1 area in the sample of male drills studied here.

In the female drills sampled, there is a significant correlation between muzzle breadth and upper M1 area, and although the correlation coefficient of upper M1 area and muzzle length was not significant, it was much higher ($r = 0.64$) than the equivalent male coefficient ($r = -0.24$). These results indicate that in females there is a link between some aspects of muzzle size and overall body size. Sexual dimorphism in the *Mandrillus* cranium is likely to come about both from ontogenetic scaling and from divergence in the male and female growth trajectories late in development (O'HIGGINS & COLLARD, 2002). If male and female growth trajectories in mandrills and drills diverge towards the end of development (O'HIGGINS & COLLARD, 2002), taken here to mean during late adolescence, and if there is a relationship between muzzle size and overall body size in male mandrills during puberty (WICKINGS & DIXSON, 1992b), it is possible that muzzle sizes in male *Mandrillus* scale, like those of females, with body mass until just prior to full adulthood. Thus, complete expression of sexual dimorphism in the male drill cranium may not occur until the animal is fully mature.

A distinctive feature of the *Mandrillus* muzzle that is not found in such a pronounced form in other large papionins is the development in males of laterally-positioned bony ridges, commonly known as paranasal swellings. Females lack the extreme paranasal swellings evident in males. Paranasal swellings are likely to be important secondary sexual characteristics, but in *M. sphinx* there is no obvious relationship between paranasal swelling size and social status (WICKINGS & DIXSON, 1992a). There is, however, a relationship between facial colouration and social status in these animals (WICKINGS & DIXSON, 1992a; SETCHELL & DIXSON, 2001). Drills and mandrills differ markedly in facial colouring, with drills lacking the bright blue paranasal and red nasal colours characteristic of mandrills. Unfortunately, there are very few published studies of the biology and sociality of wild or semi-wild *M. leucophaeus* groups, so it remains to be seen whether, in the absence of bright facial colouration, paranasal swelling size and shape are related to social status in drills. In addition, there is a lack of research relating bony muzzle morphology to mate choice and preference in *Mandrillus*, although recent work on antler size and complexity in red deer (*Cervus elephus*) indicates that antlers 'honestly' advertize relative testes size and sperm velocity (MALO *ET AL.*, 2005). Secondary sexual characteristics in male mammals therefore may act as a signal of reproductive potential to females and other males (MALO *ET AL.*, 2005). It is thus possible that bony paranasal swellings in male drills and mandrills advertize reproductive potential to females as well as to male rivals.

In overall cranial morphology, male mandrills follow similar developmental trajectories to other members of the papionin tribe (O'HIGGINS & COLLARD, 2002), but due to the distinctiveness of the *Mandrillus* paranasal region there is no papionin benchmark for growth of the paranasal swellings. Significant correlations were found between paranasal swelling breadths at M2 and M3 and also between paranasal swelling heights. These relationships reflect the distinctive 'ridge' of the paranasal swellings. There was no significant correlation between paranasal swelling breadth and height at either M2 or M3. It is suggested from this that bony development of the paranasal region in drills does not follow a regular pattern. The breadth of the paranasal swellings at M2 and M3 in the Cameroonian drill sample are bimodally distributed (Figure 3), in contrast to the other, normally distributed, craniofacial and dental dimensions. If a bimodal distribution was evident in muzzle dimensions or in paranasal swelling heights, it would suggest the presence of two distinct morphotypes, and this concept could be investigated further in future research. In the absence of extensive evidence for two morphotypes, however, a simpler explanation for the non-normal distribution in paranasal swelling breadth is that it reflects developmental irregularity.

In the male *M. leucophaeus* sample, there is no significant linear relationship between paranasal swelling size (height or breadth) and the body mass proxies upper M1 area and greatest skull length. This result is similar to that reported for *M. sphinx*, where the width and convexity of the paranasal swellings do not correlate with body size (WICKINGS & DIXSON, 1992a & b). Thus, it appears that alongside a weak relationship between overall muzzle size and body size, there is also a weak relationship between paranasal morphology and body size both in drills and mandrills. However, paranasal swelling height at M2 and M3 was significantly correlated with muzzle length, and paranasal swelling breadth at M3 was related to muzzle breadth at M2. These results indicate that although overall body size may not influence paranasal swelling size, there might be a link between the growth of the muzzle and the development of the paranasal swellings. Further research is required to assess this, and to investigate whether paranasal swelling and muzzle development is linked to the growth of other parts of the facial skeleton.

On visual inspection, the bone of the male paranasal swellings is highly vascularized and vermiculate (*sensu* OYEN *ET AL*., 1981), quite unlike much of the surrounding bone of the cranium. Although very little research has been conducted into the mechanisms and nature of vermiculate bone growth in *Mandrillus* species, it is found in a wide range of primates, and is associated with fast-growing parts of the skull (OYEN *ET AL*., 1981). It is thus likely that the growth of the paranasal swellings is rapid, reinforced by the observation that in male mandrills there is marked development of the paranasal swellings during and after puberty (WICKINGS & DIXSON, 1992b). It has been shown in male mandrills that whereas muzzle length and paranasal convexity increase linearly with body size during puberty, they grow disproportionately in adult males (WICKINGS & DIXSON, 1992b). Thus, it is possible that as well as being rapid, bone growth in the muzzle and paranasal regions in males is highly individualized, departing from a previously defined growth trajectory once full adulthood is reached. One mechanism by which this could be effected is through the influence of androgens, known to influence bone growth, with male animals having more robust bones than females (see review by COMPSTON, 2001). If the bone of the muzzle does reflect reproductive quality, as analogy with antlers in red deer (MALO *ET AL*., 2005) might suggest, bone growth could by influenced by testes size and sperm motility via androgen production. Male sex hormones clearly impact upon soft tissue morphology in *Mandrillus* (SETCHELL & DIXSON, 2001), with dominance rank also being related to development in juvenile males (SETCHELL & DIXSON, 2002), but to date there is little or no evidence linking the morphology or size of the muzzle to the effects of a rapid growth spurt just prior to maturity or to hormonal influences.

In conclusion, it is suggested from the results of this study that there is no simple relationship either between muzzle size and overall body size or between paranasal swelling size and body size in male drills (*M. leucophaeus*). This is line with research undertaken on the other extant member of the genus, the mandrill (*M. sphinx*). It is also suggested that the secondary bone growth on the drill muzzle, leading to the appearance of distinctive paranasal swellings, is rapid and irregular. This conclusion is reinforced by visual inspection of the bone of the paranasal swellings, which is vermiculate. Further work is needed to investigate the importance of the muzzle and paranasal swellings as secondary sexual characteristics in *Mandrillus*. This should include an examination of whether the bone of the muzzle and paranasal swellings acts as an indicator of reproductive potential. Attention should also be paid to the mechanisms and trajectories of muzzle bone growth in *Mandrillus*, particularly the role of androgens in male bone development.

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Table 1: The means and standard deviations of the craniodental dimensions used in analysis, alongside the results of the t-tests.

	Female		Male		
	N	Mean ± sd	N	Mean ± sd	t-values, p-values
Greatest skull length (mm)	7	150.4 ± 9.4	18	207.5 ± 9.1	-13.9, $p < 0.001$
Muzzle length (mm)	7	75.4 ± 7.1	26	110.9 ± 7.7	-11.0, $p < 0.001$
Muzzle breadth at M3 (mm)	7	46.1 ± 2.4	27	57.7 ± 2.3	-11.7, $p < 0.001$
Muzzle breadth at M2 (mm)	7	37.3 ± 4.5	27	50.2 ± 4.7	-6.5, $p < 0.001$
Muzzle breadth at P3 (mm)	6	36.5 ± 2.6	24	54.1 ± 3.3	-12.1, $p < 0.001$
Upper M1 breadth (mm)	6	9.0 ± 0.4	24	9.6 ± 0.5	-2.5, $p < 0.05$
Upper M1 length (mm)	7	9.8 ± 0.3	24	10.2 ± 0.8	-2.5, $p < 0.05$
Upper M1 area (mm^2)	6	87.6 ± 4.0	24	98.0 ± 10.0	-4.0, $p < 0.01$
Paranasal swelling breadth at M3 (mm)			27	20.1 ± 2.9	
Paranasal swelling breadth at M2 (mm)			26	13.0 ± 2.7	
Paranasal swelling height at M3 (mm)			26	4.5 ± 2.2	
Paranasal swelling height at M2 (mm)			26	6.6 ± 2.2	

Table 2: Matrix of correlation co-efficients (r) and sample sizes (N) for key variables: whole sample (pooled males and females) and female sample.

	Muzzle breadth at P3		Muzzle breadth at M2		Muzzle breadth at M3		Upper M1 area	
	Whole sample	Females	Whole sample	Females	Whole sample	Females	Whole sample	Females
Muzzle length	N = 30, r = 0.60**	N= 6, r = 0.73	N = 33, r = 0.48*	N = 7, r = 0.24	N = 33, r = 0.63**	N = 7, r = 0.65	N = 29, r = 0.33	N = 6, r = 0.64
Greatest skull length	N = 24 r = 0.75**	N = 6, r = 0.92*	N = 25, r = 0.71**	N = 7, r = 0.26	N = 25, r = 0.75**	N= 7, r = 0.87*	-	-
Upper M1 area	N = 26, r = 0.50*	N = 5, r = 0.98*	N = 30, r = 0.22	N = 6, r = 0.28	N = 30, r = 0.32	N = 6, r = 0.85*	-	-

*indicates a statistically significant correlation at the 0.05 level

**indicates a statistically significant correlation at the 0.001 level

Table 3: Matrix of correlation co-efficients (r) and sample sizes (N) for key variables: male sample.

	Muzzle breadth at P3	Muzzle breadth at M2	Muzzle breadth at M3	Muzzle length	Greatest skull length	Upper M1 area	Paranasal swelling breadth at M2	Paranasal swelling height at M3
Muzzle length	N = 24, r = 0.31	N = 26, r = -0.02	N = 26, r = 0.32	-	-	-	-	-
Greatest skull length	N = 18, r = 0.45	N = 18, r = 0.35	N = 18, r = 0.35	-	-	-	-	-
Upper M1 area	N = 21, r = 0.27	N = 24, r = -0.1	N = 24, r = 0.08	N = 23, r = -0.24	-	-	-	-
Paranasal swelling breadth at M2	N = 23, r = 0.39	N = 26, r = 0.34	N = 26, r = 0.31	N = 25, r = 0.18	N = 17, r = 0.25	N = 23, r = -0.10	-	-
Paranasal swelling breadth at M3	N = 24, r = 0.29	N = 27, r = 0.41*	N = 27, r = 0.16	N = 26, r = 0.13	N = 18, r = 0.12	N = 24, r = -0.18	N = 26, r = 0.71**	N = 26, r = 0.26
Paranasal swelling height at M2	N = 23, r = 0.20	N = 26, r = 0.21	N = 26, r = 0.32	N = 25, r = 0.46*	N = 17, r = 0.38	N = 23, r = -0.14	N = 26, r = 0.27	N = 26, r = 0.83**
Paranasal swelling height at M3	N = 23, r = 0.26	N = 26, r = 0.31	N = 26, r = 0.38	N = 25, r = 0.48*	N = 17, r = 0.38	N = 23, r = -0.27	-	-

*indicates a statistically significant correlation at the 0.05 level

**indicates a statistically significant correlation at the 0.001 level

Figure 1a: Lateral view of a male *M. leucophaeus* cranium. The height of the paranasal swellings were measured between the landmarks shown (height at M3 between points 1 and 2; height at M2 between points 3 and 4, where 1 and 3 represent the most superior extension of the paranasal swelling and points 2 and 4 the most inferior).

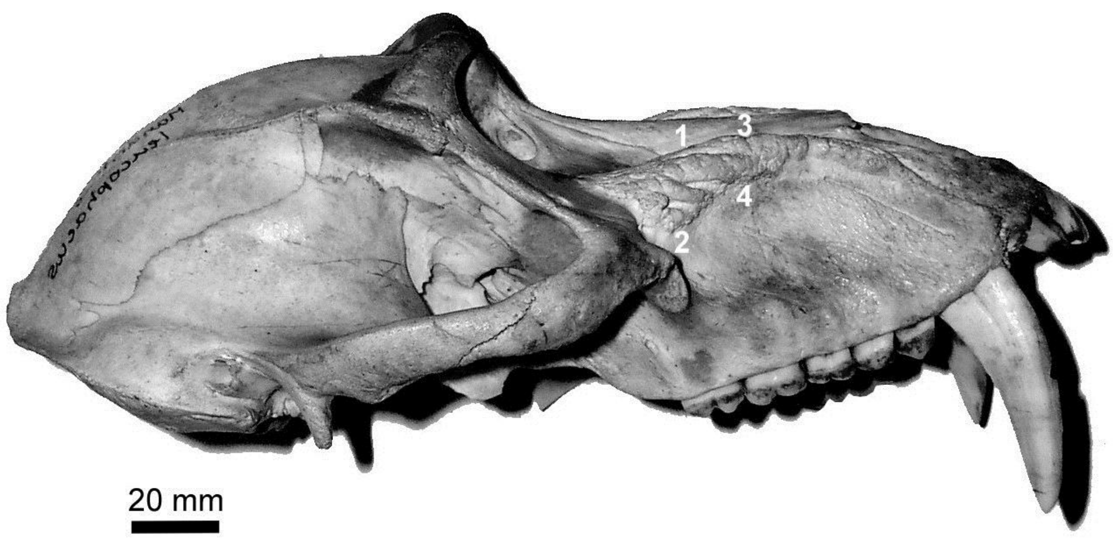

Figure 1b: Superior view of a male *M. leucophaeus* cranium. The breadth of the paranasal swellings were measured between the landmarks shown (breadth at M3 between points 1 and 2; breadth at M2 between points 3 and 4, where points 1 and 3 represent the most lateral extension of the paranasal swelling and points 2 and 4 the most medial).

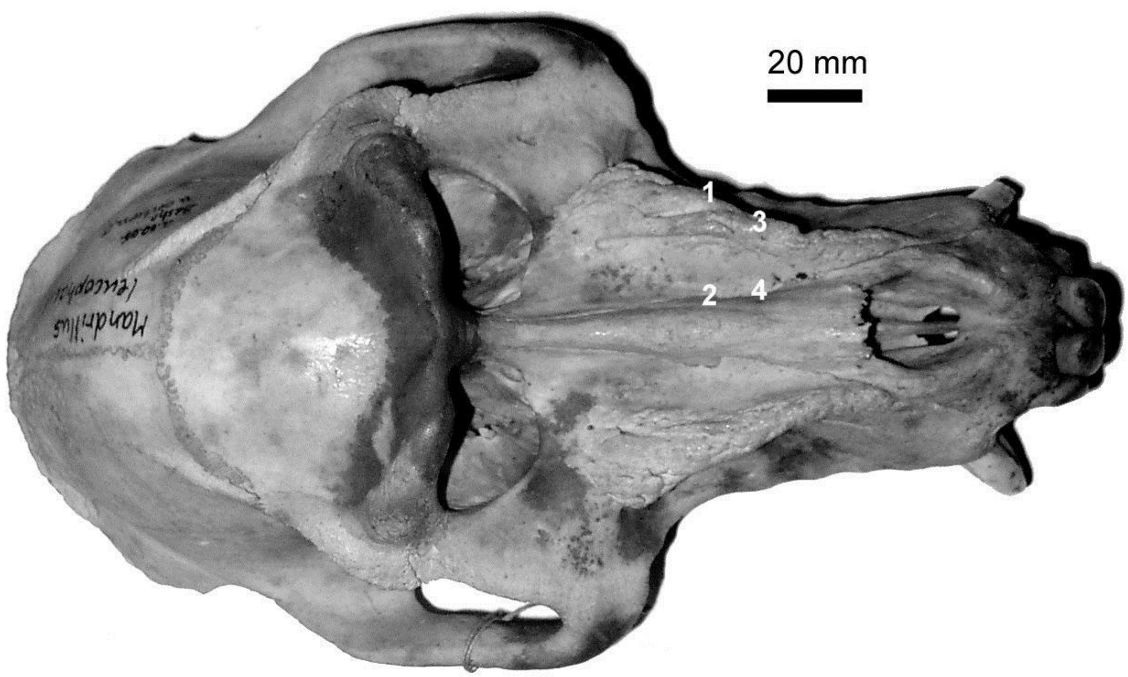

Figure 2: Relationship between muzzle length and muzzle breadth in male and female *M. leucophaeus*. Sexual dimorphism in the drill muzzle is clearly evident, and whereas there is a statistically significant correlation between muzzle length and breadth in females, this is not evident in males.

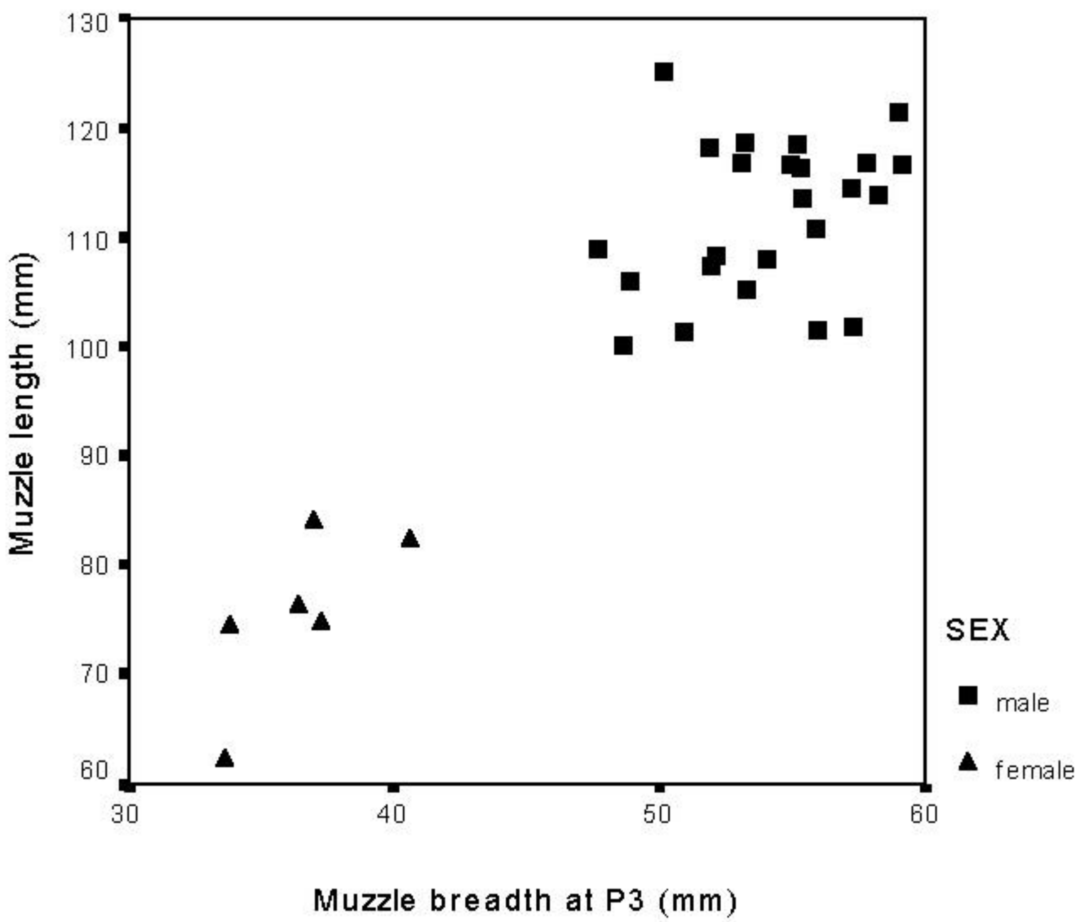

Figure 3: Histogram showing the bimodal distribution of paranasal swelling breadths at M2 in the male *M. leucophaeus* sample. A bimodal distribution is also evident in paranasal swelling breadth at M3 (not depicted). However, none of the other dimensions show such a distribution, and although the bimodal distribution of paranasal swelling breadths may represent the presence of two distinct drill morphotypes, a more extensive study is required to confirm this.